FAMILIAL RELATIONSHIPS AND BIOGEOGRAPHY OF THE WESTERN AMERICAN AND CARIBBEAN HELICOIDEA (MOLLUSCA: GASTROPODA: PULMONATA)

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ABSTRACT

Nordsieck's (1987) Revision des Systems der Helicoidea, the latest published classification of the superfamily, is further revised. By showing that anatomical characters of certain xanthonychid sub-families are as distinctive as the ones now used to designate familial rank for other helicoid families, we reaffirm Schileyko's (1978) elevating the Humboldtianinae to familial rank and we propose raising the Helminthoglyptinae, *sensu* Nordsieck, to familial rank. We support the placing of *Monadenia* by Nordsieck into a separate subfamily and we suggest that it could belong in the Bradybaenidae.

The discrete anatomical characters of the American helicoid families and their discontinuous geographical distribution bring into question the theory of a putative continuous radiation and evolution from an Asian origin. Recent geophysical data have shown that large parts of eastern Asia and western America were formed from Gondwanian terranes that migrated tectonically from the south Pacific Ocean. We suggest that most helicoid families, Asian and American, arrived at their separate destinations, passively, via these Pacifican terranes.

The classification of the land snail superfamily Helicoidea, formerly called Helicacea, has been the subject of many studies and revision within the past 50 years. Pilsbry (1939) provided the first concise key which designated the distinguishing familial characters of the Helicidae, Helicellidae, Bradybaenidae, Helminthoglyptidae, Polygyridae, Camaenidae, and Sagdidae, all of which he included in the Helicacea. Zilch (1959-1960) removed the Polygyridae and the Sagdidae from the Helicoidea and placed them in the superfamily Polygyracea (now Polygyroidea, in accordance with Article 29a of the *International Code of Zoological Nomenclature*). Solem (1978) further revised the Helicoidea by placing the Camaenidae in its own superfamily. The most recent revision of the Helicoidea was made by Nordsieck (1987) in which he recognizes the following families: Sphincterochilidae Zilch, 1960; Xanthonychidae Strebel and Pfeffer, 1880; Bradybaenidae Pilsbry, 1934; Hygromiidae Tryon, 1866; Helicidae Rafinesque, 1815.

In considering the familial relationships within a superfamily, one is naturally led to speculate on the evolution of these families from a single ancestral group and their dispersal from some point of origin to their present distribution. The most generally accepted theory on the biogeography of the Helicoicdea has been that the ancestral helicoid probably arose in the Palearctic during the Mesozoic era (Pilsbry, 1894, 1939) from whence the ancestors of the European helicoids could easily spread throughout Europe while the ancestral xanthonychids invaded the Americas via the Bering land bridge no later than early Eocene and probably earlier (Pilsbry, 1894).

We have been studying the biogeography of the western North American helicoids for many years, especially in northwest Mexico, and we have been puzzled by their total absence from a large part of Sonora where a continuous radiation would have been expected from a trans-Beringean southward radiation. We have also been puzzled by the total absence of helicoids from a large part of northwestern South America which would have had to be traversed in order to reach Peru and Argentina.

Recent determinations in geophysics that most of eastern Asia and a large part of Northwest America were not part of the Asian continent or the American continent,

respectively, during the Mesozoic, but rather were part of Gondwanian land masses located in early Mesozoic in the south-central Pacific Ocean led us to investigate the possibility that Asian and western American and Caribbean helicoids could have arrived at their present destinations via the Gondwanian terranes from a Pacifican origin. Our concurrent studies on the familial characteristics of the American helicoids have also shown that several of Nordsieck's xanthonychid subfamilies are sufficiently different, anatomically, to warrant familial status. Together, the pronounced anatomical differences and the discontinuous geographical distributions of these subfamilies have provided a compelling stimulus to investigate available evidence which could support a theory of a Pacifican origin for the superfamily. Detailed analyses and resulting determinations follow.

FAMILIAL RELATIONSHIPS

Pilsbry (1939) placed all Western American and Caribbean Helicoidea into the single family Helminthoglyptidae. He recognized no less than eight strongly differentiated groups which he ranked as subfamilies. Only seven, however, were named: Helminthoglyptinae Pilsbry, 1939; Sonorellinae Pilsbry, 1939; Humboldtianinae Pilsbry, 1939; Cepoliinae Pilsbry, 1939 (emendation for Cepolinae Hoffman, 1928, a homonym); Xanthonychinae Strebel and Pfeffer, 1879 (as Xanthonychidae); Lysinoinae Hoffman, 1928; Epiphragmophorinae Hoffman, 1928. Of these seven subfamilies, Zilch (1959-1960) lumped Lysinoinae into Humboldtianinae and Epiphragmophorinae into Helminthoglyptinae. Subsequently, Schileyko (1978) raised Humboldtianinae to familial rank.

The use of the name Helminthoglyptidae was brought into question by Baker (1959) when he showed that the name Xanthonychidae Strebel and Pfeffer, 1879 had considerable priority over Helminthoglyptidae Pilsbry, 1939. Furthermore, Baker showed in a precise chronological review of family names from 1867 to 1958 that the Old World family Bradybaenidae had been considered repeatedly to include many New World subfamilies of the Xanthonychidae. Indeed there were no precise, consistent characters that could be used to separate Bradybaenidae from Xanthonychidae. Nevertheless, Baker condescended to allow the use of the name Bradybaenidae with this statement (1959): "Since the sizes of families are matters of convenience and/or custom, we Americans, North and South, can leave to the wisdom of our Old World colleagues the advisability of a separate family for the genera of their home lands". To date, European malacologists have continued to use the name Bradybaenidae for what Baker considered to be "Old World Xanthonychidae", while many American malacologists have continued to use the name Helminthoglyptidae for New World Xanthonychidae.

All helicoid families, Old World as well as New World, are characterized by having a reproductive system equipped with a dart and mucus gland apparatus associated with or in close proximity to the vagina; certain genera in this superfamily without a dart apparatus are believed to have become secondarily simplified in their evolution from dart-bearing ancestors. The principal characters used in separating families

within the Helicoidea are the type and shape of the mucus glands and the position of their insertion into the vagina or the dart sac. Pilsbry (1939) published a simple key of distinguishing characters to differentiate each family which can be summarized as follows:

I. HELICIDAE: medium or large snails, usually with banded shells, having one dart sac with two tubular, simple or branching mucus glands inserted close to its base, the spermatheca on a long duct which usually bears a branch.

II. HELICELLIDAE (now in Hygromiidae): of medium or small size, with the dart sac often twinned, sometimes wanting, the tubular mucus glands when present inserted well above it on the vagina; spermathecal duct medium or short, never branching.

III. HELMINTHOGLYPTIDAE (now Xanthonychidae): dart sac or sacs and mucus glands present, the latter club-shaped, globular or irregular (not tubular or finger-shaped), inserted close to the base of the dart sac.

Pilsbry then briefly referred to the Bradybaenidae "of Eastern Asia" as having irregular type mucus glands opening through an accessory sac on the dart sac or sometimes directly at the base of the latter.

It was clear from the above definitions that Pilsbry's Helminthoglyptidae and Bradybaenidae were a catch-all group for those species whose mucus glands were not tubular or finger-shaped. Schileyko (1978) reviewed the superfamily Helicoidea, with emphasis on anatomical characters. He recognized that the Humboldtianinae formed a consistently distinct group characterized by four compact dart sacs arranged circumferentially high on the vagina, and four globular, compact mucus glands also arranged circumferentially above the dart sacs and inserting directly into the vagina at the level of the dart sacs. He therefore raised this subfamily to familial rank as a distinct and separable taxon whose character differences were of equal magnitude as the character differences used in separating the Helicidae and Hygromiidae. Miller (1987) agreed with Schileyko and showed that the genus *Bunnya* Baker, 1942, was characterized by a similar set of dart sacs and mucus glands, except that their number was three instead of four, and thus this genus should be included in the Humboldtianidae.

Most recently, Nordsieck (1987) published a revision of the taxonomy of the Helicoidea based on a detailed study of the dart apparatus and mucus glands of the various groups. He illustrated diagrammatically the various configurations of the system and defined each of the numerous families, subfamilies, and tribes, many of them newly erected. He then prepared an elaborate cladogram based not only on the dart apparatus and mucus glands but also on the presence or absence of accessory seminal vesicles, chromosome number, presence or absence of accessory dart sacs, presence or absence of spermathecal diverticulum, and the position of the spermatheca (either along the spermoviduct or bent away from it.).

The main thrust of Nordsieck's cladogram, however, was to concentrate on the evolution of the Helicidae, Hygromiidae, and Bradybaenidae. A similar detailed analysis would have been highly desirable for the Xanthonychidae,

although it is recognized that there are large gaps in our knowledge of anatomical characters and chromosome numbers of the numerous xanthonychid subfamilies. Nordsieck affirmed that the correct familial name for the Western American and Caribbean Helicoidea should be Xanthonychidae as Baker (1959) had shown, and he recognized the following nine subfamilies in the Americas: Monadeniinae Nordsieck, 1987; Helminthoglyptinae Pilsbry, 1939; Cepoliinae Pilsbry, 1939; Epiphragmophorinae Hoffman, 1928; Trichodiscininae Nordsieck, 1987; Lysinoinae Hoffman, 1928; Xanthonychinae Strebel and Pfeffer, 1880; Metostracinae Nordsieck, 1987; Humboldtianinae Pilsbry, 1939. By returning the Humboldtianinae to the Xanthonychidae as a subfamily, he disagreed with Schileyko's familial ranking for this group. He concurred that *Bunnya* belonged with the Humboldtianinae and erected the new tribe Bunnyini for this genus.

Nordsieck's revision of the Helicoidea provides the most authoritative classification of the superfamily at this time. Disagreements with his findings must be substantiated with evidence. In addition, the dictates of the International Code of Zoological Nomenclature must be followed if we are to avoid chaos in nomenclature.

During the past many years, we have been examining the reproductive anatomies of most of the numerous genera of the western North American helicoids and, in many cases, most or all of their individual species. The genera most throughly examined are the following: *Helminthoglypta* Ancey, 1887; *Micrarionta* Ancey, 1880; *Xerarionta* Pilsbry, 1913; *Eremarionta* Pilsbry, 1913; *Plesarionta* Pilsbry, 1939; *Monadenia* Pilsbry, 1895; *Sonorella* Pilsbry, 1900; *Sonorelix* Berry, 1943; *Mohavelix* Berry, 1943; *Tryonigens* Pilsbry, 1927; *Greggelix* Miller, 1972; and *Eremariontoides* Miller, 1981. Additional genera also critically examined but from only a few representative species are the following: *Epiphragmophora* Doring, 1875; *Averellia* Ancey, 1887; *Humboldtiana* Ihering, 1892; *Lysinoe* H. and A. Adams, 1855; *Cepolis* Montfort, 1810; *Bunnya* Baker, 1942.

In all of our examinations, we were impressed repeatedly by certain distinguishing characters that stood out markedly from all others and were consistently occurring in the species of what are now classified by Nordsieck as three subfamilies, namely the Humboldtianinae, the Helminthoglyptinae (*sensu* Nordsieck, i.e. minus *Monadenia* which had been included by Pilsbry), and the Monadeniinae. In the genus, *Humboldtiana*, all of our species had four compact, vesicular mucus glands, circumferentially arranged around the vagina and inserting directly into it; additionally, they had four dart sacs also circumferentially arranged around the vagina and located immediately below the mucus glands. This arrangement was strikingly unlike any other system found in any other helicoid except *Bunnya*. In the Helminthoglyptinae, all dart bearing species had one or both mucus glands consisting of wide membranes that wrapped around various parts of the anterior end of the reproductive tract such as the penis, and/or the vagina, and/or the artrial sac. Again, this arrangement was strikingly different from any other helicoid system. Finally, in the Monadeniinae, all species were equipped with only a single, tubular mucus gland which inserted on a large swelling

of the anterior end of the reproductive tract, a structure somewhat resembling the accessory sac (Nordsieck's Nebensack) found in some of the Bradybaenidae. Although Pilsbry (1939) considered the anterior muscular swelling to be simply an atrium, the similarity with the bradybaenid accessory sac could not be ignored; furthermore, the tubular mucus gland would, by Pilsbry's own definition, exclude this subfamily from the Xanthonychidae.

We came to the conclusion, therefore, that the anatomical differences found in the Humboldtianinae and in the Helminthoglyptinae were as distinctive and of equal or greater magnitude as those now used to designate familial rank for other helicoid families, namely Helicidae, Hygromiidae, Bradybaenidae, and Sphincterochilidae. Accordingly, we concur with Schileyko that the Humboldtianinae should be raised to familial rank. We further propose that the Helminthoglyptinae, *sensu* Nordsieck, also be raised to familial rank. Because Miller (1970, 1973, 1981) already provided evidence that certain genera in Pilsbry's Sonorellinae (Nordsieck's Sonorellini) probably arose from different helminthoglyptine ancestors, namely *Mohavelix* Berry from *Helminthoglypta micrometalleoides* Miller, 1970, and *Eremariontoides* Miller from *Eremarionta greggi* Miller, 1981, the Sonorellini must be considered polyphyletic and unacceptable as a taxon. To date, there are no convincing data available to indicate the immediate dart-bearing ancestors of *Sonorella* Pilsbry, *Sonorelix* Berry, *Greggelix* Miller, and *Tryonigens* Pilsbry. Classification of the helminthoglyptid genera at the subfamilial level, therefore, will have to await more sophisticated methods of analysis probably involving chromosome banding and DNA hybridization. Finally, we also concluded that the Monadeniinae were more closely similar, anatomically, to the Bradybaenidae than to the Xanthonychidae, Humboldtianidae, or Helminthoglyptidae so that they should be classified either as a bradybaenid subfamily or raised to familial rank. At this time, we recommend the conservative approach of leaving them in subfamilial status as a fourth bradybaenid subfamily along with Bradybaeninae Pilsbry, 1924, Aegistinae Kuroda and Habe, 1955, and Helicostylinae Ihering, 1909.

A simple key can be erected as follows to separate the Humboldtianidae and the Helminthoglyptidae from the Xanthonychidae:

1. One or more mucus glands membranous . . . .
. . . . Helminthoglyptidae
   Mucus glands vesicular 2
2. Mucus glands and dart sacs compact, multiple, seated high on the vagina . . . . Humboldtianidae
   Mucus glands and dart sacs not thus . . . .
. . . . Xanthonychidae

Additionally, figure 1 shows the most probable phylogeny of the families, based on the concept that membranous mucus glands are probably ancestreal to vesicular glands.

In summary, the classification of the Western American and Caribbean Helicoidea, lumped by Nordsieck (1987) into the single family Xanthonychidae, is now proposed as follows:

Helicoidea Rafinesque
    Xanthonychidae Strebel and Pfeffer
        Cepoliinae Pilsbry
        Epiphragmophorinae Hoffman
        Trichodiscininae Nordsieck
        Lysinoinae Hoffman
        Xanthonychinae Strebel and Pfeffer
        Metostracinae Nordsieck
    Humboldtianidae Pilsbry
        Humboldtianinae Pilsbry
        Bunnyinae Nordsieck
    Helminthoglyptidae Pilsbry
    Bradybaenidae Pilsbry
        Monadeniinae Nordsieck

BIOGEOGRAPHY

After determining that the anatomical characteristics of the Western American and Caribbean Helicoidea were sufficiently distinct to separate at least four different families, namely Xanthonychidae, Bradybaenidae, Humboldtianidae, and Helminthoglyptidae, our attention turned to their possible evolution and ultimate dispersal from a common origin. Figure 2 shows the general distribution of the Western American and Caribbean Helicoidea and their East Asian relatives. To account for this nearly circum-Pacific distribution, many terrestrial malacologists theorized that these helicoids had a Eurasian origin and migrated into the Americas via a Bering land bridge during the Tertiary period (Pilsbry, 1894; Pilsbry, 1948; Gregg, 1959). This theory seemed to us to leave too many important questions unanswered. For example, in order to attain the current distribution in the Americas (Fig. 2), the theory presumed a long and narrow dispersal along the west coast of North America into Mexico and Central America followed by a radiation eastward to the main Caribbean islands as well as many of the lesser Antilles, ultimately as far as the Bahamas and southern Florida. In the meantime, however, these helicoids failed to reach the central and eastern United States although there is ample evidence that during that same time period the Polygyridae were able to populate extensive areas from southern Florida to New England to Washington, Oregon, and northern California and nearly all of central and western Mexico. The Helicoidea also would have crossed the isthmus of Panama to reach vast areas of Peru and northwestern Argentina but they failed to leave any trace in Panama, Colombia, and Ecuador; they also failed to disperse into Venezuela and Brazil. More recently, as a result of a five year study of helminthoglyptid distribution in Sonora, Mexico, by one of us (ENG), we found a complete absence of helminthoglyptids from the latitude of Hermosillo to the Sinaloan border (Naranjo-García, 1988); yet we found that region to be well populated by other families of large snails such as bulimulids and polygyrids. Such gaps in distribution, unexplainable by geological or ecological events due to the presence of other families of large snails in these gaps, presented a serious flaw in the theory of a Bering land bridge migration.

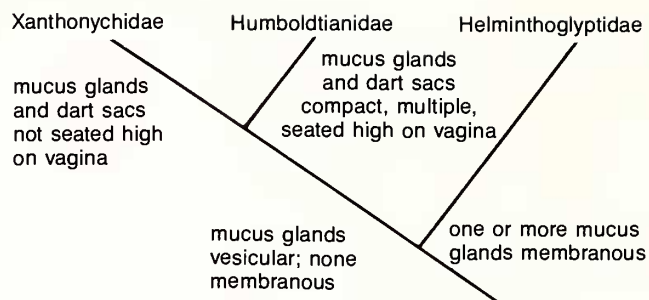During the past four decades, several biogeographers

Fig. 1. Probably phylogeny.

began to question the widely invoked theories of palearctic origins for much of the New World biota. Croizat (1952) and Melville (1966, 1981) suggested that the exchange of biota through a Bering land bridge was relatively insignificant. Melville (1966), in order to explain the distribution of angiosperms along the Pacific Rim, proposed the existence of a mesozoic land mass in the south-central Pacific, which he named Pacifica, that broke up and migrated tectonically to accrete to the continental margins of Asia and America. Nur and Ben-Avraham (1977) suggested that the circum-Pacific mountain belts could have been the result of past continental collisions similar to those associated with the Alpine belt. They proposed that these collisions were made by parts of a continental mass situated in the South Pacific Ocean, Pacifica (referring to Melville's 1966 article), which disaggregated during the Mesozoic and spread out on the Kula, Farallon, Phoenix, and Pacific plates eventually to reach continental margins. Subsequently, additional geophysical and geological evidence appeared in the literature in support of the former existence of Pacifica (Kamp, 1980; Davis et al., 1978; Coney et al., 1980; McGeary and Ben-Avraham, 1981; Nur and Ben-Avraham, 1982). Then Jones et al. (1982) showed convincing evidence, supported by the work of Tarduno et al. (1986), that western North America consists of accreted terranes which originated thousands of kilometers to the south and west of their present position. Jones et al. also provided evidence to show that Permian terranes, originally formed in the Tethys Sea, had also accreted to form a large part of eastern Asia. Kulm et al. (1986), while studying the subduction zone of Oregon and Washington which possesses accreted terranes, found communities of clams and tube worms (Calyptogena sp.) similar to those found in the accretionary complexes of Japan, the Philippine Plate, and other locations around the Pacific Ocean. Figure 3 is a schematic composite model of Pacifica land mass migrations during the Mesozoic era, according to these cited authors.

In the light of this mounting volume of evidence, we studied the possibility that the circum-Pacific Ocean distribution of the Helicoidea could be much better explained by theorizing a center of origin on a Mesozoic Pacifican land mass, Pacifica, which broke up into several parts that were ultimately carried, as Nur and Ben-Avraham suggested, to form large parts of western North and South America and east Asia. These terranes provided a passive means of dispersal for ancestral populations of helicoids to dock at various
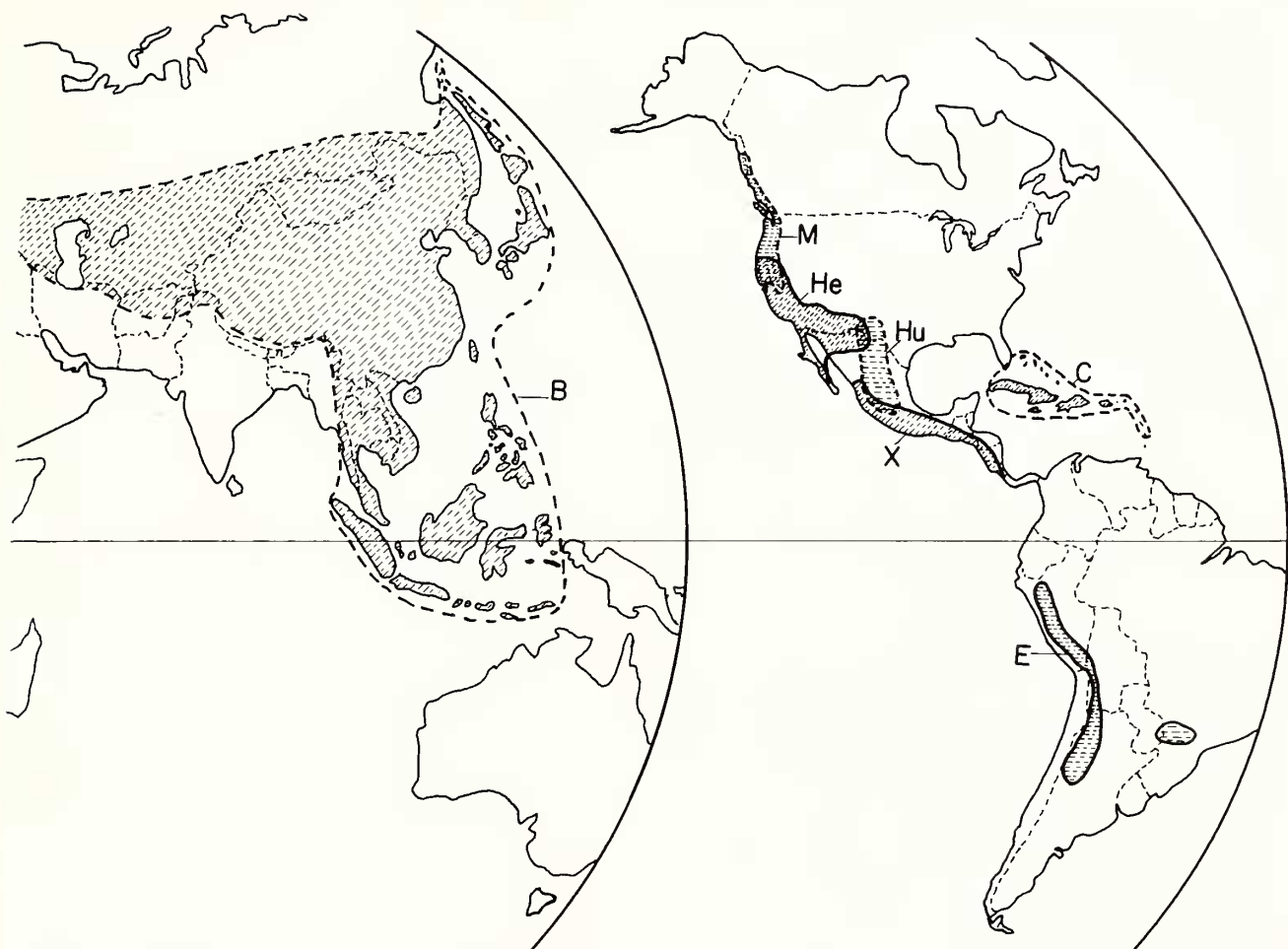
Figure 2. Approximate areas of distribution of Western American and Caribbean Helicoidea and Asian Bradybaenidae: B, Bradybaenidae (other than Monadeniinae); C, Cepoliinae (Xanthonychidae); E. Epiphragmophorinae (Xanthonychidae); He, Helminthoglyptidae; Hu, Humboldtianidae; M, Monadeniinae (Bradybaenidae); X, Xanthonychidae (other than Cepoliinae and Epiphragmophorinae).

discrete parts of the Americas and Asia. With this theory, the absence of any Helicoidea from Panama, Colombia, Ecuador, and a large area of Sonora did not need to be attributed to mass extinctions. Moreover, the time period involved in the break-up and migration of the Pacifican terranes during the Mesozoic would have permitted ample isolation for the evolution of separate families and subfamilies on each different terrane.

We came to the conclusion that the Pacifican theory did indeed better explain the circum-Pacific distribution of the helicoids than the trans-Beringean theory. To explain the current distribution of the families and subfamilies of these helicoids, we hypothesize the following vicariance patterns: 1) the arrival of the ancestral Bradybaenidae in eastern Asia, with subsequent dispersal along the shore of the Tethys Sea to south-central Asia and into southern Europe; 2) the arrival of the ancestral Helminthoglyptidae in western North America, docking along what is now California and Baja California, with eventual dispersal eastward as far as west Texas and Chihuahua; 3) the arrival of the ancestral Xanthonychidae, other than Epiphragmophorinae and Cepoliinae, along the

shores of southwestern Mexico and Central America; 4) the arrival of the ancestral Epiphragmophorinae in the vicinity of Peru, with eventual dispersal southeasterly as far as northwest Argentina and southern Brazil; 5) the arrival of the ancestral Cepoliinae into the Caribbean region on the Greater Antilles terranes which Burke et al. (1984) stated had origins in the Pacific Ocean during the Mesozoic and migrated to collide with the Bahamas long before the formation of the Isthmus of Panama.

In the case of the Humboldtianidae, conchological and anatomical characters indicate a closer evolutionary relationship to the European helicoids than to the other American helicoids (Schileyko, 1978). Additionally, their widespread distribution not only over the entire Mexican Plateau but also, as fossils, as far north as east-central Wyoming led us to hypothesize that they must have been indigenous to the North American craton after it separated from Laurasia. They are, therefore, the one American helicoid family that apparently did not evolve from Pacifican ancestors.

Although the theory of a Pacifican origin for the East Asian, Caribbean, and Western American helicoids (except-
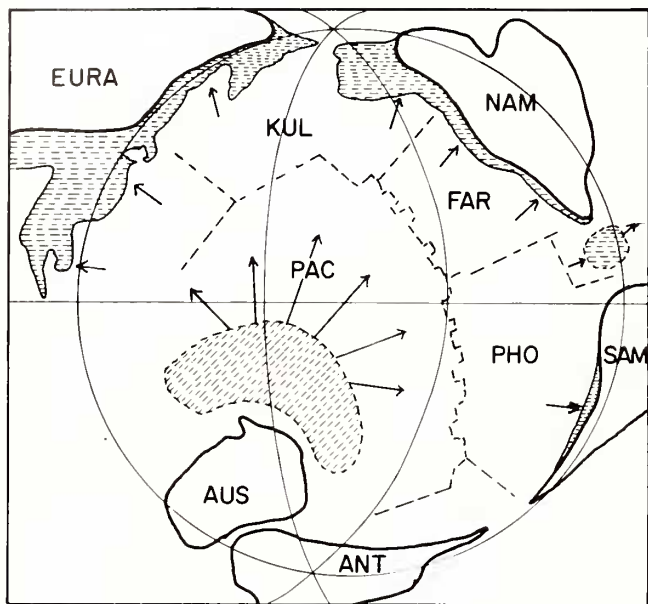
Figure 3. Schematic composite model of estimated Pacifica land mass migrations during Mesozoic era. Heavy lines mark estimated positions of continental areas at end of Mesozoic, according to Dietz and Holden (1975). Horizontal dashed lines mark presumed Pacifican terranes that accreted to the continents according to Jones et al. (1982) and Burke et al. (1984). Diagonal dashed lines mark estimated position of Pacifica at beginning of Mesozoic according to Nur and Ben-Avraham (1977). Major Pacific plates during Mesozoic according to Zonenshayn et al. (1984): ANT, Antarctica; AUS, Australia; EURA, Eurasia; FAR, Farallon plate; KUL, Kula plate; NAM, North America; PAC, Pacific plate; PHO, Phoenix plate; SAM, South America.

ing the Humboldtianidae) satisfactorily explains the distribution of the current populations, it does not rule out the possibility of some limited Tertiary trans-Beringean migration. As stated earlier, we consider the Monadeniinae to be more closely related to the Bradybaenidae than to any other American helicoid group. The possibility exists, therefore, that this bradybaenid subfamily could have migrated across the Bering land bridge from northeast Asia. Conchological characters would support a very close relationship between Japanese *Euhadra* species and *Monadenia* species. Anatomically, however, the Monadeniinae are very different from Japanese *Euhadra* or from northeast Siberia *Bradybaena*. Accordingly, it appears to us that the ancestral Monadeniinae evolved on a separate Pacifican terrane that ultimately docked on the North American continent somewhere on the Canadian or southern Alaskan coast.

ACKNOWLEDGMENTS

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